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Land-use intensity and biodiversity effects on infiltration capacity and hydraulic conductivity of grassland soils in southern Germany

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Abstract

Evidence from experimental and established grasslands indicates that plant biodiversity can modify the water cycle. One suspected mechanism behind this is a higher infiltration capacity (ν_B) and hydraulic conductivity (K) of the soil on species-rich grasslands. However, in established and agriculturally managed grasslands, biodiversity effects cannot be studied independent of land-use effects. Therefore, we investigated in established grassland systems how land-use intensity and associated biodiversity of plants and soil animals affect ν_B and K at and close to saturation. On 50 grassland plots along a land-use intensity gradient in the Biodiversity Exploratory Schwäbische Alb, Germany, we measured ν_B with a hood infiltrometer at several matrix potentials and calculated the saturated and unsaturated K. We statistically analysed the relationship between ν_B or K and land-use information (e.g., fertilising intensity), abiotic (e.g., soil texture) and biotic data (e.g., plant species richness, earthworm abundance). Land-use intensity decreased and plant species richness increased ν_B and K, while the direction of the effects of soil animals was inconsistent. The effect of land-use intensity on ν_B and K was mainly attributable to its negative effect on plant species richness. Our results demonstrate that plant species richness was a better predictor of ν_B and K at and close to saturation than land-use intensity or soil physical properties in the established grassland systems of the Schwäbische Alb.

KEYWORDS
Biodiversity Exploratories, land use, plant diversity, ROSETTA, soil animals

1 | INTRODUCTION

Land-use intensification is a major driver of global biodiversity loss (Butchart et al. 2010; Foley et al. 2005; Sala et al. 2000). Declining biodiversity threatens ecosystem functions and services like nutrient cycling and provisioning of fresh water (Cardinale et al. 2012; Isbell et al. 2011; Soliveres et al. 2016). Up to now only little attention has been given to the role of biodiversity for soil erosion and flood generation. Both, soil erosion and flood generation are driven by the capability of soils to take up (infiltration) and conduct water to deeper soil layers (hydraulic conductivity). A high infiltration capacity (i.e., maximum infiltration rate under a given matrix potential) reduces the risk of surface runoff and thus soil erosion. A high hydraulic conductivity facilitates the storage of water in the deeper soil, which mediates the time until rainwater reaches groundwater or a stream and thus affects flood generation. It has been shown that infiltration capacity and hydraulic conductivity are directly influenced by land use (e.g., Bormann & Klaassen, 2008; Zhou et al. 2008). Recent results from experimental grassland and a chronosequence of community succession in semiarid grassland furthermore suggest that plant diversity increases the infiltration capacity and hydraulic conductivity (Fischer et al. 2015; Liu et al. 2019). However, the relationship between land-use intensity, biodiversity, and the infiltration capacity and hydraulic conductivity of soils of established, agriculturally managed grassland is still unclear.

Grassland is one of the major land-use types in the European Union and Germany and covers over 20 % of their areas (EUROSTAT, 2017). Key properties of grassland soils, which determine the water balance of these ecosystems are infiltration and hydraulic conductivity. Infiltration capacity and hydraulic conductivity depend on texture, bulk density, stone content, and organic matter concentration of the soil. While texture rarely changes because of land use, bulk density and soil organic matter concentration can vary considerably with land management. The soil organic matter concentration of grassland is usually positively affected by fertiliser application because of the stimulation of above- and belowground biomass production (Conant et al. 2001). Grazing can increase primary production and manure input and thus have a positive effect on soil organic matter concentration on sites with a long history of grazing, while slightly negative effects have been reported for sites without such a grazing history (Conant et al. 2001). Soil organic matter favours soil aggregation and decreases bulk density and subsequently increases the infiltration capacity (Fischer et al. 2015; Franzluebbers, 2002; Liu et al. 2019). Therefore, differences in soil organic matter concentration between land-use systems on soils with otherwise comparable properties can lead to differences in the infiltration capacity (Bormann & Klaassen, 2008; Zhou et al. 2008). Animal treading during grazing and the use of heavy machines for fertiliser application or mowing can lead to soil compaction, which decreases the infiltration capacity and surface-near hydraulic conductivity because macropores are destroyed (Ankeney et al. 1990; Fatichi et al. 2014; Leitinger et al. 2010). Additionally, trafficking of the soil reduces the earthworm biomass and can reduce the burrow length (Schrader & Larink, 2003). Earthworm burrows and root channels are important controls of macroporosity and thus influence infiltration capacity (Ankeney et al. 1990; Fischer et al. 2014). Apart from the presence or absence of specific land-use measures (e.g., with or without fertilisation), soil hydrological properties probably also vary with land-use intensity (e.g., the amount and frequency of fertiliser application). For example, the root biomass decreased and soil aggregation increased with increasing land-use intensity (Barto et al. 2010), which likely has consequences for the infiltration capacity and hydraulic conductivity.

The biodiversity of plants and animals can influence several ecosystem processes including soil hydrological processes (Decaëns et al. 2006; Soliveres et al. 2016; Weisser et al. 2017). Soil animals play an important role for soil hydrology because they construct differently sized and long pores. Thus, the effect of soil animals on water infiltration varies with the present animal species and associations of species (Lavelle, 1997) and possibly with the diversity and abundance of soil animals. Animals constructing relatively large pores (e.g., earthworms) can modify mainly the infiltration capacity very close to saturation, i.e. when the largest pores participate in water transport (Fischer et al. 2014). Smaller animals (e.g., Pauropoda) might serve as indicators for the occurrence of small pores, which are relevant for the infiltration capacity at lower matrix potentials. A higher soil animal diversity could therefore indicate a higher number of soil pores and larger variation in pore sizes, which would increase infiltration capacity and hydraulic conductivity at different matrix potentials. Increasing plant diversity, measured as plant species richness, has been shown to decrease actual evapotranspiration from topsoil on Central European grasslands, while actual evapotranspiration from subsoil increased (Leimer et al. 2018). This finding could neither be explained by variations in aboveground biomass, controlling transpiration, nor by plant cover, controlling soil evaporation via shading, with plant diversity. Therefore, Leimer et al. (2018) hypothesised that a higher infiltration capacity and a higher hydraulic conductivity of the soils on species-rich grassland sites led to increased downward water fluxes from topsoil to subsoil and thus to the observed soil depth partitioning of evapotranspiration. The positive relationship between plant species richness and infiltration capacity of experimental grassland, where plant diversity was manipulated, was attributed to changes in bulk density and soil organic carbon (Fischer et al. 2015). An increase in root biomass with increasing plant species richness (Ravenek et al. 2014) might also lead to more available macropores for water transport. The root traits and thus the pore size and length distribution in soil might also be modified by the functional plant diversity because some plants form, for example, deep-reaching and relatively large tap-roots, like many herbs, while others have a shallow and dense rooting system, like grasses. Different combinations of such root traits might result in different infiltration capacities. However, in a biodiversity experiment, functional plant diversity did not affect infiltration capacity while the effects of presence or absence of grasses and legumes remained unclear (Fischer et al., 2014, 2015).

In contrast to experiments, in which biodiversity is artificially varied, biodiversity in established and agriculturally managed

grassland is driven by land-use practices like fertilisation, grazing, and mowing. Land use strongly affects the abundance and diversity of soil animals (Birkhofer et al. 2012; Decaëns et al. 2006), plant species richness, and plant functional group composition (Socher et al. 2012) in these grassland systems. Fertiliser application usually decreases plant species richness while it increases biomass (Crawley et al. 2005; Gough et al. 2000; Socher et al. 2012). Fertiliser application can also increase the cover of grasses, proportion of grass species, and reduce the proportion of herb species (Socher et al., 2012, 2013). Grazing intensity, livestock types, and mowing frequency can further influence plant species richness and functional composition although the directions of these effects vary with the studied region (Collins et al. 1998; Klaus et al. 2013; Socher et al. 2013; Zechmeister et al. 2003). To the best of our knowledge, there are no studies in established, agriculturally managed grassland systems that investigated the effect of land-use intensity in combination with biodiversity on infiltration capacity and hydraulic conductivity.

The main objective of our study was to determine if biodiversity affects the infiltration capacity (ν_B) and the saturated (K^*) and unsaturated (K_u) hydraulic conductivity near saturation of soils in established and agriculturally managed grassland systems. (1) We hypothesise that land-use intensity has the strongest effect and decreases ν_B, K^*, and K_u because of increased soil compaction. (2) According to previous findings in manipulative biodiversity experiments, we further hypothesise that plant diversity and the diversity and abundance of soil animals have a positive effect on ν_B, K^*, and K_u. (3) We expect the effect of land-use intensity on ν_B, K^*, and K_u to be partly mediated by physical soil properties like bulk density or organic carbon concentration as a measure of soil organic matter concentration.

2 | METHODS

This study was conducted as part of the 'Biodiversity Exploratories' project (www.biodiversity-exploratories.de) in Germany in the region Schwäbische Alb. The Schwäbische Alb is situated in the low mountain ranges of southwestern Germany on calcareous bedrock (Jurassic limestone) with geomorphic karst forms (elevation of studied plots: 521–816 m, annual mean temperature: 6–7°C, soils: Leptosols and Cambisols) (Fischer et al. 2010). The soil texture is rich in clay (on average 54%, minimum 15% and maximum 71%). We investigated 50 agriculturally managed grassland plots (each 50 m × 50 m) varying in land-use intensity (for details see Fischer et al. 2010).

2.1 | Infiltration measurements

Between 26 September and 20 October 2017, we measured the infiltration capacity near saturation on each of the 50 grassland plots in-situ with a hood infiltrometer (UGT, Müncheberg, Germany; method described in Schwärzel & Punzel, 2007). We chose this method because it does not disturb the soil or damage the measurement site (like bore holes for example), which was of particular importance for the plots located in a nature reserve and for preservation of the plots for the long-term Biodiversity Exploratories project.

The measurements were carried out using a hood with a radius of 11.4 cm which was placed on the soil surface inside a metal ring with a radius of 12.4 cm. The vegetation within the metal ring was cut to 1–2 cm height. The space between the ring and the hood was sealed with wet fine sand. Subsequently, the hood was flooded and the hydraulic pressure head in the water volume under the hood was controlled via a Mariotte water supply system. The applied pressure head, i.e. matrix potential (Ψ_M) or tension (h), was measured using a U-tube manometer. The steady-state infiltration was recorded after three constant readings from the infiltration reservoir of the Mariotte water supply system. At $\Psi_M = 0$ cm, the soil is saturated and all pores can participate in water flow, while at $\Psi_M = -2.0$ cm the largest active pores can be estimated to have an approximate equivalent diameter of 1.5 mm, which further decreases to approximately 0.75 mm at $\Psi_M = -4$ cm (Jarvis et al. 1987). On each plot, we measured the infiltration at the matrix potentials $\Psi_M = -0.1$ and -2.0 cm. The matrix potential was then further decreased in 2 cm steps and infiltration measured until the bubble point of the soil was reached. The bubble point of the soil represents the matrix potential at which air permeates through a pore channel into the hood, i.e. the minimum matrix potential that can be applied at the respective site. On a few plots with especially slow infiltration and high bubble point, we did not measure all matrix potential steps up to the bubble point. On one randomly selected plot (AEG23), we performed three separate measurements along a transect to check representativeness of the infiltration measurements. The three measured values for ν_B at $\Psi = -0.1$ cm ranged between 9.3 and 36.3×10^{-6} m s^{-1}. Compared to the range of all ν_B measurements at $\Psi = -0.1$ cm (1.7–433.1×10^{-6} m s^{-1}), the range of the measurements on AEG23 is small (only 6% of the range of all plots) and thus, we considered a single measurement per plot to be sufficient.

2.2 | Land-use intensity, biotic and abiotic data

A number of land-use, biotic, and abiotic variables were measured on the same 50 grassland plots (i.e., within the same 50 m × 50 m areas in which the infiltration measurements were done), which have the potential to influence infiltration capacity and hydraulic conductivity. The potential explanatory variables, investigated in this study, are summarised in Table 1.

Fertiliser application rates (kg N ha^{-1} year^{-1}), mowing frequency (cuts year^{-1}), and livestock units d ha^{-1} year^{-1} were obtained from yearly interviews with farmers and land owners (Vogt et al. 2019). We used data from 2012 to 2016, averaged across years to eliminate the effect of random variations between years. From this data set, the standardised individual land-use intensity components fertilising intensity, mowing intensity, and grazing intensity were calculated according to Blüthgen et al. (2012). The individual components were then aggregated to a continuous land-use intensity index (LUI) (Blüthgen et al. 2012).

TABLE 1 Median, minimum and maximum of land-use, biotic and abiotic properties of the 50 study plots

		Median	Minimum	Maximum
Land use	Grazing intensity	0.6	0.0	6.8
	Mowing intensity	0.9	0.0	2.3
	Fertilising intensity	0.2	0.0	7.5
	Land use intensity index	1.7	0.7	3.1
Plants	Plant species richness	31.1	20.0	55.0
	Evenness	0.8	0.6	0.8
	Shannon index of plants	2.6	1.7	3.2
	Number of herb species	16.9	9.2	34.2
	Number of grass species	9.4	5.5	15.4
	Number of legume species	3.6	1.2	7.2
	Cover of herbs (%)	43.0	21.4	83.9
	Cover of grasses (%)	66.0	31.4	91.1
	Cover of legumes (%)	7.7	1.0	27.5
	Total plant cover (%)	120.2	78.9	147.9
	Cover bryophytes (%)	14.1	0.0	67.0
	Aboveground plant biomass (g m^{-2})	233.0	27.9	523.3
	Fine root biomass (<2 mm) (g cm^{-3})	0.9	0.1	5.7
	Root decomposition (October–April) (%)	11.6	3.6	23.5
Animals, bacteria, fungi	Shannon index of Myriapoda	0.5	0.0	1.4
	Earthworm abundance (individuals m^{-2})	382.0	32.0	987.0
	Pauropoda abundance (individuals m^{-2})	191.0	0.0	2610.0
	Symphyla abundance (individuals m^{-2})	318.0	0.0	1814.0
	Centipede abundance (individuals m^{-2})	32.0	0.0	302.0
	Invertebrate biomass (nmol FAME g^{-1} soil)	3.3	1.4	5.5
	Microbial biomass C (μg g^{-1} soil)	756.3	391.4	1193.1
	Fungal biomass (nmol FAME g^{-1} soil)	13.8	5.4	28.8
Abiotic properties	Slope (°)	6.1	1.5	16.6
	Soil depth (cm)	25.5	12.0	63.0
	Soil type (n)	Cambisols (17) and Leptosols (33)		
	Stone content (% g g^{-1})	1.7	0.0	13.9
	Bulk density (g cm^{-3})	0.9	0.6	1.0
	Clay content (%)	57.1	14.6	70.8
	Sand content (%)	4.1	0.8	19.9
	Soil pH	6.3	5.3	7.6
	Total C concentration (g kg^{-1} soil)	67.4	40.6	105.5
	Inorganic C concentration (g kg^{-1} soil)	0.6	0.3	54.3
	Organic C concentration (g kg^{-1} soil)	65.0	40.2	91.3

Abbreviation: FAME, fatty acid methyl esters.

Vegetation was recorded annually from 2012 to 2016 on each plot. We estimated the cover of all vascular plant species on 4 m × 4 m from mid-May to mid-June and calculated plant species richness as the number of plant species per 16 m^2. Furthermore, we determined the number of species within each of the plant functional groups grasses, legumes, and herbs. From these data, Shannon index of diversity H' and evenness J' were calculated according to Equations (1) and (2), where p_i is the proportional plant cover of species i and S is the number of species (Socher et al. 2013).

$$H' = -\sum(p_i \cdot ln(p_i)) \quad (1)$$

$$J' = H'/ln(S) \quad (2)$$

In addition, cover of all vascular plants and bryophytes was estimated and cover sums of the functional groups grasses, legumes, and herbs were calculated by summing up the cover of all species in the respective groups. Although plots were regularly managed by resident farmers, temporary fences ensured that no mowing or grazing took place prior to sampling (Klaus et al. 2013). Aboveground community biomass was sampled by cutting the vegetation at a height of 0.02–0.03 m in four 0.5 m × 0.5 m subplots. Biomass was oven dried for 48 h at 80°C, weighed immediately after drying, and averaged per plot. To eliminate the effect of random variations between years, the mean values of the vegetation variables of five years (2012–2016) were used for statistical analysis. Fine root biomass (<2 mm) within the upper 10 cm of the mineral soil was determined in May 2011. Soil core samples were taken from 14 single points per plot and combined for the analysis (total soil volume of 2747.5 cm^3). Root samples (diameter <2 mm) were cleaned from soil residues with distilled water under a 500 μm sieve, dried at 40°C, and weighed. Decomposition of fine roots (<2 mm) within the upper 10 cm of the mineral soil was measured between October 2011 and April 2012 with the litterbag method. The litterbags consisted of polyester with a mesh size of 100 μm and were filled with herbaceous roots (Solly et al. 2014). After leaving three replicates in the soil for 6 months, mass loss as measure of root decomposition was determined.

In April 2011, the abundances of Myriapoda and earthworms were determined by collecting soil cores with a diameter of 20 cm. The upper 5 cm of one core were extracted according to a modified Kempson heat extraction protocol. The abundance of Chilopoda, Diplopoda, Pauropoda and Symphyla were counted from this sample. The Shannon index was calculated for Chilopoda and Diplopoda species. The upper 10 cm of two additional soil cores were hand searched for 1 h for earthworms. For further details see Birkhofer et al. (2012).

In May 2014, 14 soil samples from 0–10 cm depth were taken per site using core augers (diameter 56 mm). Soil samples were pooled, sieved <2 mm and stored at −20°C within 8 h after sampling. We determined microbial biomass C using the chloroform fumigation extraction method (CFE) according to Vance et al. (1987) with modifications according to Keil et al. (2011). C was extracted from each fumigated and non-fumigated replicate (10 g) with 40 ml 0.5 M K_2SO_4. The suspension was horizontally shaken (30 Min, 200 rpm) and centrifuged (30 min, 4400 · *g*). Fumigated sample replicates were incubated with $CHCl_3$ for 24 h prior to extraction. C concentrations in dissolved (1:3 v/v extractant:H_2Odeion.) extracts were measured with a TOC/TN analyser (Multi N/C 2100S, Analytik Jena AG, Jena, Germany). Microbial biomass C, in μg g^{-1} dry soil, was calculated as difference between fumigated and non-fumigated replicate. Microbial community structure was assessed on 2 g of field moist soil using phospholipid fatty acid (PLFA) analyses according to Frostegård et al. (1991) as described in detail in Boeddinghaus et al. (2019). PLFA FAMEs (nmol FAME g^{-1} dry soil) were assigned to microbial groups according to Ruess and Chamberlain (2010): a15:0, i15:0, i16:0, and i17:0 together with cy17:0 and cy19:0 as well as 16:1ω7 were used to represent soil bacteria, while PLFA FAME 18:2ω6,9 served as a fungal indicator and FAME 20:4ω6 was used as a marker for invertebrates.

The average slope over the area of each plot was determined (Fischer et al. 2010). The soil type was characterised according to the World Reference Base for Soil Resources (IUSS, Working Group WRB, 2007) and soil depth was measured as the maximum drilling depth (Fischer et al. 2010; Schöning et al. 2016). Soil texture of the upper 10 cm of the mineral soil was determined by dispersion of soil aggregates into discrete units and separation of soil particles of different size by sieving and sedimentation (DIN-ISO 11277) (Fischer et al. 2010). Soil pH (0.01 M $CaCl_2$) was measured in 2017 in mineral soil samples from the 0–10 cm soil layer, following the same sampling and preparation approach as the sampling in 2014. On the mixed samples taken in 2014, we determined: Soil bulk density (BD) as g cm^{-3} using the sampled soil volume and the dry soil weight (without stones, soil dried minimum 72 h at 60°C); stone content in g g^{-1} dry soil after removal of roots; total C, inorganic C, and organic C concentrations. Air-dried, sieved to <2 mm, and ground samples were measured by dry combustion at a temperature of 1100°C and subsequent determination of evolving CO_2 with a Thermal Conductivity Detector (TCD), Elemental analyser/CN analyser (VarioMax, Elementar, Hanau). Inorganic carbon was measured after removal of organic carbon at a temperature of 450°C for 16 h.

2.3 | Data preprocessing and statistical analyses

The infiltration capacity at a specific matrix potential is directly related to the hydraulic conductivity (Wooding, 1968). Although it can be argued that the assumptions of the Richards equation are not met in natural soils, we calculated the saturated (K^*) and unsaturated (K_u) hydraulic conductivity according to Wooding (1968). For this purpose, Gardner's coefficient α was calculated according to Equation (3) from measured infiltration capacities ν_B at two different, adjacent matrix potentials ($\Psi_i \in \{-0.1, -2.0, -4.0, -6.0\ \text{cm}\}$) at the same location.

$$\alpha_i = ln\left(\frac{\nu_{B_i}}{\nu_{B_{i+1}}}\right)/(\Psi_i - \Psi_{i+1}) \tag{3}$$

The unsaturated hydraulic conductivity was then calculated per matrix potential using Equation (4) and the radius of the infiltration surface (a = 12.4 cm).

$$K_{u_i} = \nu_{B_i}/\left(1 + \frac{4}{\pi \cdot \alpha_i \cdot a}\right) \tag{4}$$

The saturated hydraulic conductivity was finally calculated according to Gardner (1958) with Equation (5) using $\Psi = -0.1$ cm, K_u and α as calculated from measurements at $\Psi = -0.1$ and -2.0 cm.

$$K^* = K_u/e^{\alpha \cdot \Psi} \tag{5}$$

On one plot (AEG21) the measurement at $\Psi = -2.0$ cm and at one plot (AEG19) the measurement at $\Psi = -4.0$ cm had to be discarded. Therefore, K^* and K_u at $\Psi = -0.1$ cm on AEG21 were

calculated from the measurements at $\Psi = -0.1$ cm and -4.0 cm and K_u at $\Psi = -2.0$ cm on AEG19 from measurements at $\Psi = -2.0$ and -6.0 cm. Accordingly, there are no values for ν_B and K_u at $\Psi = -2.0$ cm for AEG21 and at $\Psi = -4.0$ cm for AEG19 (Table 2). The dataset of ν_B, K^*, and K_u is published as Leimer and Wilcke (2021).

To obtain a complete dataset, a missing value in the variable stone content was replaced with a measurement from 2007 on the same plot (AEG06). A missing root decomposition value (AEG11) was replaced with the mean value of the other 49 plots.

All statistical analyses were done with the R 3.4.3 software package (R Core Team, 2017). Data was Box-Cox transformed (1 was added to variables that contained zeros) using the R package *car* (Fox & Weisberg, 2011) to approximate normal distribution. The employed transformation per variable can be found in Supporting Information Table S1. Pearson correlations were calculated between transformed continuous variables and a *t*-test was calculated, if a factorial variable was included. We performed an Akaike information criterion (AIC)-based linear model selection to identify, which of the potential explanatory variables presented in Table 1 explain best ν_B and K_u at $\Psi = -0.1$, -2.0, -4.0 and -6.0 cm, and K^*. Using the transformed data, we performed a forward linear model selection with the function *setpAIC()* (Venables & Ripley, 2002) starting with the constant null model. We decided to do forward model selection instead of backward model selection to minimise the influence of collinearity between the explanatory variables. Model selection was regarded as complete, if none of the remaining potential explanatory variables would have improved the AIC by at least 1. For ν_B at $\Psi = -6.0$ cm, the number of selectable variables was limited to three because only 15 observations were available.

We used the software ROSETTA (Schaap et al. 2001) to estimate saturated hydraulic conductivity (K^*) from soil physical properties. ROSETTA is widely used and has implemented a set of pedotransfer functions to derive $K^*_{ROSETTA}$ from clay, sand, and silt content and bulk density of the soil. We compared K^*, calculated from our infiltration measurements, with K^*, predicted by the selected linear model, and $K^*_{ROSETTA}$, respectively, using Pearson correlations to determine, if a function with biotic or abiotic variables can better predict K^* in our study region.

Structural equation modelling (SEM) allows testing direct and indirect relationships between variables in a multivariate approach (Grace, 2006). SEM was performed to test the hypotheses that LUI affects ν_B at $\Psi = -0.1$ cm and K^*, respectively, via the respective selected variables plant species richness, fungal biomass, Shannon index of Myriapoda or soil organic C concentration, and root decomposition (Table 3). The residual variances of fungal biomass and plant species richness were allowed to be correlated by including a covariance structure in the SEMs. To represent the influence of site conditions on the selected plant and soil variables in the SEMs, we included slope, soil depth, sand and clay content, stone content, soil pH, and soil inorganic C concentration. We did not include direct paths from the site conditions to ν_B and K^*, respectively, because these relationships were not significant (Table S2) and this would have led to too many paths in the model. Including or excluding the site conditions did not change the overall SEM results. For the SEMs, data was transformed and scaled, if necessary, as given in Table S1. The adequacy of the models was determined via χ^2 tests and root mean square error of approximation (RMSEA). SEM was performed in R using the function *sem()* from the package *lavaan* (Rosseel, 2012).

3 | RESULTS

ν_B at $\Psi = -0.1$ cm ranged from 1.7 to 433.1×10^{-6} m s^{-1} with a median of 54.4×10^{-6} m s^{-1}. K^* ranged from 1.2 to 308.3×10^{-6} m s^{-1} with a median of 30.5×10^{-6} m s^{-1}. With decreasing matrix potential, ν_B and K_u decreased (Table 2). ν_B at $\Psi = -6.0$ cm and K_u at $\Psi = -4.0$ cm were not significantly ($p < 0.05$) correlated with any of the potential explanatory variables (Table S2) and therefore not considered in the further evaluation. ν_B, K^*, and K_u were not significantly correlated with the physical soil properties stone content, bulk density, clay and sand content, pH, and total, inorganic and organic C concentration (Table S2, Figure S1). Only ν_B at $\Psi = -0.1$ cm was marginally significantly and at $\Psi = -2.0$ cm significantly negatively correlated with soil depth (Table S2).

3.1 | Land-use effects on ν_B, K^* and K_u

Land-use intensity (LUI) correlated significantly negatively with ν_B at $\Psi = -0.1$ cm, K^*, and K_u at $\Psi = -0.1$ and -2.0 cm, and marginally

TABLE 2 Median, minimum and maximum of infiltration capacity (ν_B) and saturated (K^*) and unsaturated (K_u) hydraulic conductivity in 10^{-6} m s^{-1} at different matrix potentials (Ψ)

	Median	Minimum	Maximum	Number of observations
K^* ($\Psi = 0$ cm)	30.5	1.2	308.3	50
K_u ($\Psi = -0.1$ cm)	29.7	1.2	294.9	50
K_u ($\Psi = -2.0$ cm)	28.4	2.3	110.7	34
K_u ($\Psi = -4.0$ cm)	14.7	6.0	54.0	14
ν_B ($\Psi = -0.1$ cm)	54.4	1.7	433.1	50
ν_B ($\Psi = -2.0$ cm)	46.6	1.0	425.0	49
ν_B ($\Psi = -4.0$ cm)	42.3	7.8	393.9	34
ν_B ($\Psi = -6.0$ cm)	28.5	11.2	380.9	15

TABLE 3 Selected explanatory variables for infiltration capacity (ν_B) and saturated (K^*) and unsaturated (K_u) hydraulic conductivity at different matrix potentials (Ψ)

		df	Explained variation	Residual df	Unexplained variation	AIC	Relation
K^* ($\Psi = -0$ cm)	Null model			49	88.5	30.5	
	Plant species richness	1	27.3	48	61.2	14.1	+
	Shannon index of Myriapoda	1	4.9	47	56.3	11.9	+
	Fungal biomass	1	4.4	46	51.9	9.8	−
	Root decomposition	1	3.1	45	48.8	8.7	+
$\mathbf{K}_u$ ($\Psi = -0.1$ cm)	Null model			49	88.1	30.3	
	Plant species richness	1	27.1	48	61.0	13.9	+
	Shannon index of Myriapoda	1	4.8	47	56.2	11.9	+
	Fungal biomass	1	4.4	46	51.8	9.8	−
	Root decomposition	1	3.2	45	48.7	8.6	+
$\mathbf{K}_u$ ($\Psi = -2.0$ cm)	Null model			33	32.1	0.1	
	Number of grass species	1	10.2	32	21.9	−10.9	+
	Pauropoda abundance	1	7.1	31	14.8	−22.2	+
$\mathbf{K}_u$ ($\Psi = -4.0$ cm)	Null model			13	7.2	−7.4	
	Pauropoda abundance	1	1.5	12	5.7	−8.6	+
	Number of grass species	1	2.7	11	3.0	−15.6	+
ν_B ($\Psi = -0.1$ cm)	Null model			49	83.7	27.7	
	Plant species richness	1	17.1	48	66.6	18.3	+
	Fungal biomass	1	4.9	47	61.7	16.5	−
	Root decomposition	1	4.2	46	57.5	15.0	+
	Soil organic C concentration	1	4.0	45	53.6	13.4	+
ν_B ($\Psi = -2.0$ cm)	Null model			48	87.9	30.6	
	Plant species richness	1	14.5	47	73.3	23.8	+
	Fungal biomass	1	5.3	46	68.0	22.0	−
	Soil depth	1	4.7	45	63.3	20.5	−
ν_B ($\Psi = -4.0$ cm)	Null model			33	24.2	−9.6	
	Earthworm abundance	1	6.6	32	17.6	−18.5	−
	Number of legume species	1	3.9	31	13.6	−25.1	+
	Soil inorganic C concentration	1	1.7	30	11.9	−27.7	−
	Evenness	1	1.7	29	10.2	−30.8	+
ν_B ($\Psi = -6.0$ cm)[a]	Null model			14	10.7	−3.1	
	Centipede abundance	1	2.4	13	8.3	−4.9	−
	Clay content	1	2.6	12	5.7	−8.6	+
	Fine root biomass	1	1.4	11	4.3	−10.7	+

Note: The column names indicate the degrees of freedom used by the explanatory variables (df) and remaining after fitting the respective variable (Residual df), the explained and unexplained variation of the data, the Akaike information criterion (AIC) and the relationship between the dependent variables and the explanatory variables (+, positive; −, negative).

[a]Limited to three explanatory variables due to only 15 data points.

significantly with ν_B at $\Psi = -2.0$ cm (Figure 1). The LUI components mowing intensity and fertilising intensity also correlated significantly negatively with ν_B ($\Psi = -0.1$, -2.0 and -4.0 cm), K^*, and K_u ($\Psi = -0.1$ and -2.0 cm; Table S2 and Figure S1). The LUI component grazing intensity correlated marginally significantly or significantly positively with ν_B ($\Psi = -0.1$, -2.0 and -4.0 cm) and K_u ($\Psi = -2.0$ cm; Table S2).

3.2 | Effects of biotic properties on ν_B, K^* and K_u

ν_B ($\Psi = -0.1$, -2.0 and -4.0 cm), K^*, and K_u ($\Psi = -0.1$ and -2.0 cm) increased significantly with increasing plant species richness, Shannon index of plants, number of herb, grass, and legume species, and cover of bryophytes (Table S2, Figure S1). Cover of grasses correlated significantly negatively with K^* and K_u at $\Psi = -0.1$ cm (Table S2 and

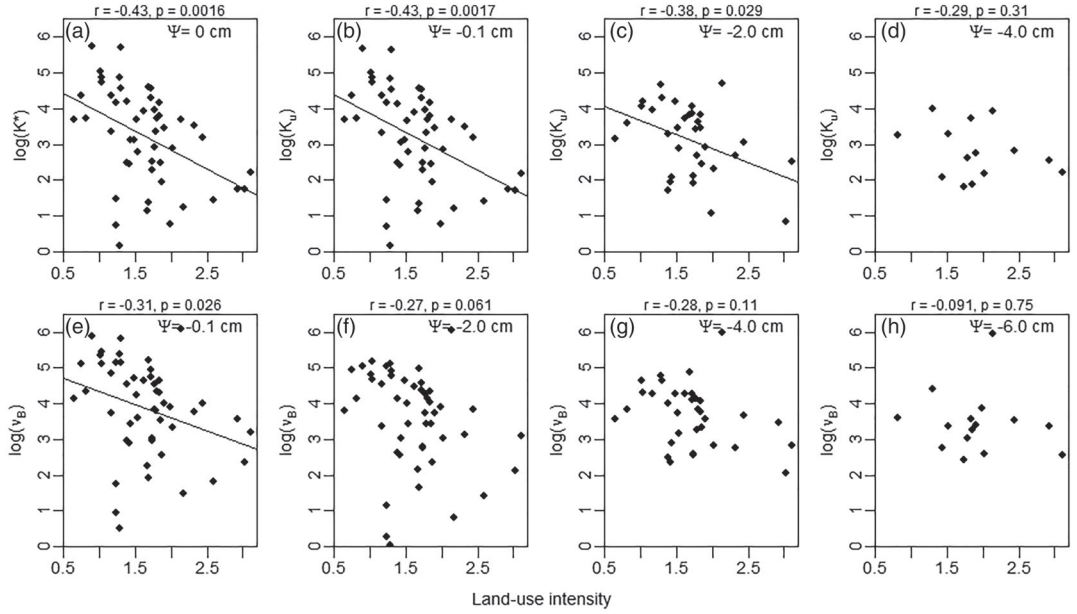

FIGURE 1 Relationship between land-use intensity and (a) saturated hydraulic conductivity (log_e-transformed K^* in 10^{-6} m s^{-1}), (b–d) unsaturated hydraulic conductivity (log_e-transformed K_u in 10^{-6} m s^{-1}) and (e–h) infiltration capacity (log_e-transformed ν_B in 10^{-6} m s^{-1}) at different matrix potentials (Ψ). The values for *r* and *p* represent the results of a Pearson correlation. Regression lines are shown for significant ($p < 0.05$) relations and for illustration purpose only

Figure S1). Aboveground biomass also correlated significantly negatively with ν_B ($\Psi = -0.1$ and -2.0 cm), K^*, and K_u ($\Psi = -0.1$ cm). Fine root biomass did not and root decomposition did at most marginally signficantly positively correlate with ν_B, K^*, and K_u (Table S2).

The Shannon index of Myriapoda significantly increased K^* and K_u at $\Psi = -0.1$ cm. The Pauropoda abundance also correlated positively with ν_B ($\Psi = -0.1$ (, -2.0,) and -4.0 cm), K^*, and K_u ($\Psi = -0.1$ and -2.0 cm), while the centipede abundance showed only few marginally significant correlations with ν_B, K^*, and K_u (Table S2 and Figure S1). Invertebrate biomass correlated significantly negatively with K^* and K_u ($\Psi = -0.1$ cm). ν_B, K^*, and K_u did not correlate with fungal biomass and only marginally significantly negatively with microbial biomass C (Table S2, Figure S1).

3.3 | Linear models for ν_B, K^* and K_u

The model selection procedure resulted in several biotic and few abiotic variables being selected as explanatory variables. However, neither LUI nor any of its components were selected as explanatory variable in the model selection procedure for ν_B, K^*, and K_u at the different matrix potentials (Table 3). Soil depth was selected as an explanatory variable of ν_B ($\Psi = -2.0$ cm; Figure 2h). Furthermore, soil organic C concentration was among the selected explanatory variables for ν_B ($\Psi = -0.1$ cm; Figure 2g), soil inorganic C concentration for ν_B ($\Psi = -4.0$ cm; Figure 2k), and clay content for ν_B ($\Psi = -6.0$ cm; Figure 2n), although these variables alone did not correlate significantly with ν_B (Table 3).

K^* and K_u ($\Psi = -0.1$ cm) were best explained by a model with plant species richness, Shannon index of Myriapoda, fungal biomass and root decomposition as explanatory variables (Table 3 and Figure 2a–d), although fungal biomass was not significantly correlated with K^* and K_u. These variables explained together 45% of the variation in K^* and K_u ($\Psi = -0.1$ cm), respectively. For ν_B ($\Psi = -0.1$ cm), the same variables were selected except for soil organic C concentration instead of the Shannon index of Myriapoda (Table 3 and Figure 2g), although fungal biomass and soil organic C concentrations were not significantly correlated with ν_B at any matrix potential. Also, the model for ν_B ($\Psi = -2.0$ cm) contains plant species richness and fungal biomass. The selected models for K_u ($\Psi = -2.0$ and -4.0 cm) consist of the biotic explanatory variables number of grass species and Pauropoda abundance (Figure 2e,f), despite their non-significant correlation with K_u at $\Psi = -4.0$ cm. During the model selection for ν_B ($\Psi = -4.0$ and -6.0 cm), further biotic variables were selected: earthworm abundance, number of legume species, evenness, centipede abundance, fine root biomass—although fine root biomass was not significantly correlated with ν_B at $\Psi = -6.0$ cm (Table 3 and Figure 2i,j,l,m,o).

The estimation of K^* with ROSETTA using soil texture and bulk density resulted in values ranging from 6.2 to 33.1×10^{-6} m s^{-1} with a median of 12.7×10^{-6} m s^{-1}. $K^*_{ROSETTA}$ did not correlate with K^*, calculated from infiltration measurements (Figure S2a).

3.4 | Mediators of land-use effects on ν_B and K^*

The structural equation models indicated that the negative effects of land-use intensity on ν_B at $\Psi = -0.1$ cm and K^* were mediated by plant species richness, as the direct path from land-use intensity to ν_B at

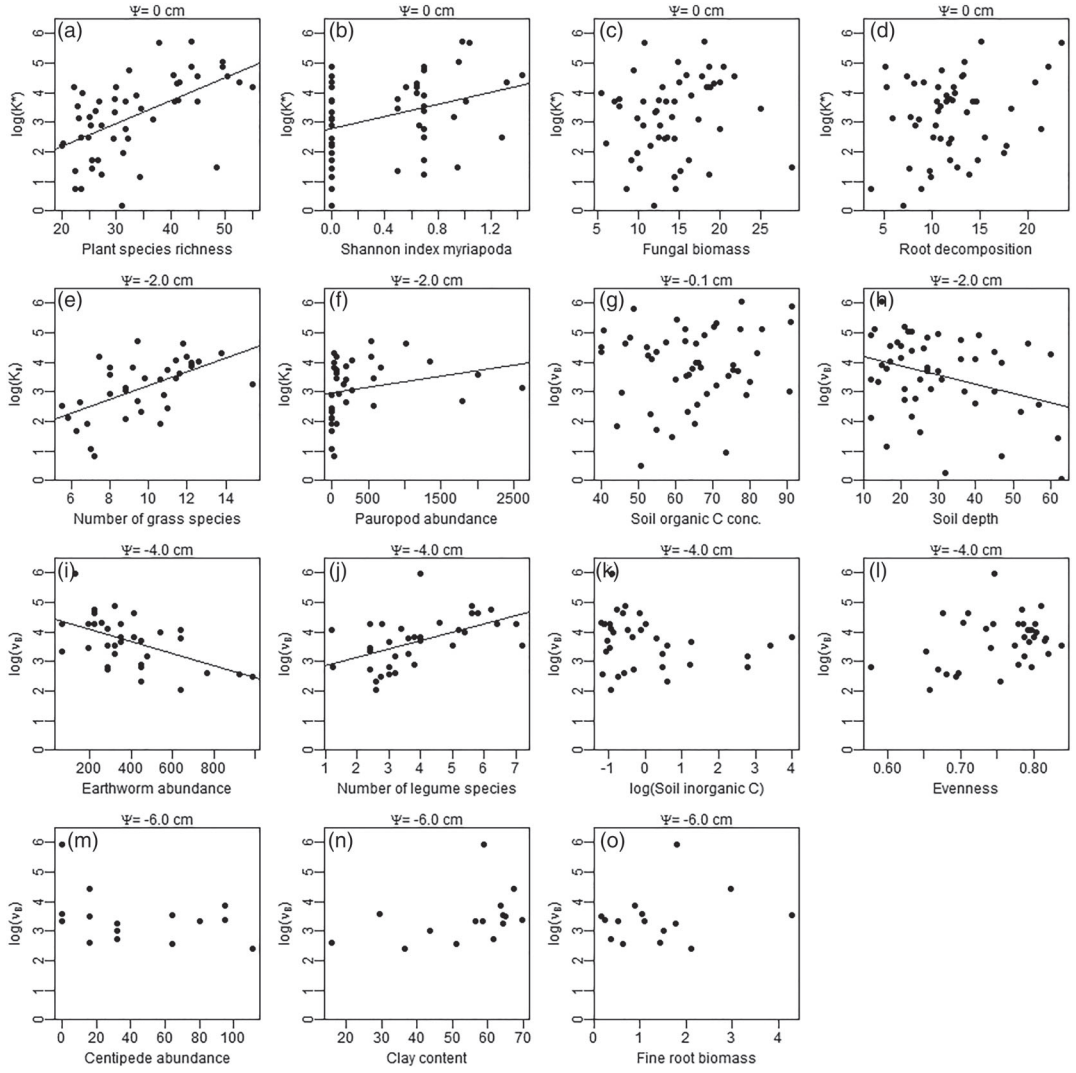

FIGURE 2 Relationship between selected explanatory variables (see Table 3) and (a–d) saturated hydraulic conductivity (log_e-transformed K^* in 10^{-6} m s^{-1}), (e–f) unsaturated hydraulic conductivity (log_e-transformed K_u in 10^{-6} m s^{-1}) at matrix potential $\Psi = -2.0$ cm, and (g–o) infiltration capacity (log_e-transformed ν_B in 10^{-6} m s^{-1}) at $\Psi = -0.1$ cm (g), $\Psi = -2.0$ cm (h), $\Psi = -4.0$ cm (i-l) and $\Psi = -6.0$ cm (m–o). Regression lines are shown for significant ($p < 0.05$) relations and for illustration purpose only

$\Psi = -0.1$ cm and K^*, respectively, was not significant (Figures 3 and 4). The paths from LUI to plant species richness and fungal biomass were significant and indicated negative effects, while the paths to the Shannon index of Myriapoda (in the case of K^*)/soil organic C concentration (in the case of ν_B at $\Psi = -0.1$ cm) and root decomposition were not significant (Figures 3 and 4, Table S4 and S5). The paths from soil pH to plant species richness and fungal biomass as well as the paths from stone content to Shannon index of Myriapoda (all positive path coefficients) and from soil depth to soil organic C concentration (negative path coefficient) were significant. The paths from sand content to fungal biomass and clay content to soil organic C concentration were marginally significant. The paths from plant species richness and Shannon index of Myriapoda to K^* were significant and the path from root decomposition to K^* marginally significant with positive path coefficients. Therefore, the only series of significant paths from LUI to K^* was via plant species richness. In the SEM for ν_B at $\Psi = -0.1$ cm, the paths from plant species richness, fungal biomass, and soil organic C concentration to ν_B at $\Psi = -0.1$ cm were significant and the path from root decomposition marginally significant. As the direct path from LUI to ν_B at $\Psi = -0.1$ cm was not significant and land-use intensity had a positive effect on ν_B ($\Psi = -0.1$ cm) via fungal biomass, the negative land-use intensity effect on ν_B ($\Psi = -0.1$ cm) was also mediated by plant species richness. According to a χ^2 test, the data on ν_B at $\Psi = -0.1$ cm ($\chi^2 = 4.1$, $p = 0.98$) and K^* ($\chi^2 = 5.9$, $p = 0.92$), respectively, did not significantly deviate from the structural equation model. The RMSEA was not significantly different from zero for both models.

4 | DISCUSSION

The obtained values for K^* are in the range of common values for clay-rich soils (Blume et al. 2016). Results for K^* and K_u

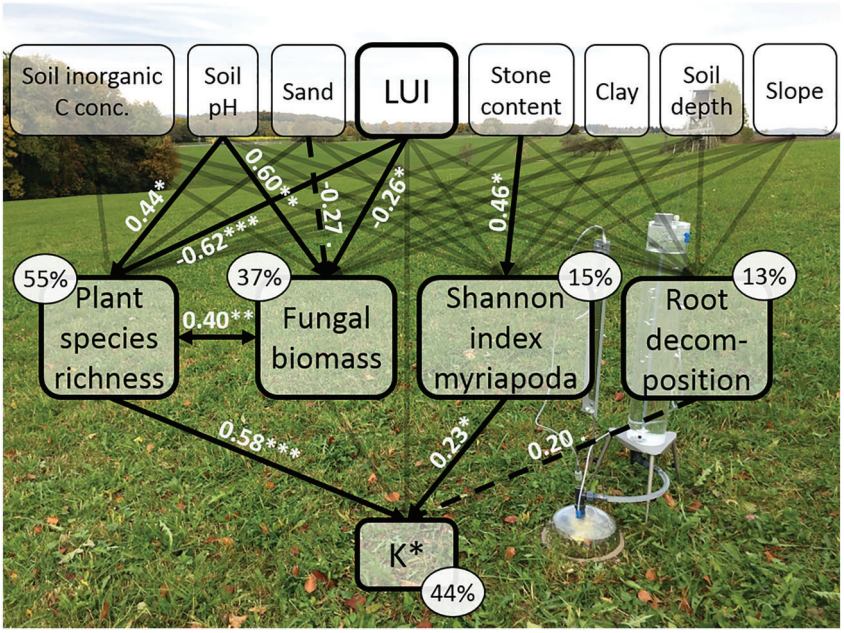

FIGURE 3 Structural equation model (SEM) of the effect of land-use intensity (LUI) via selected variables on saturated hydraulic conductivity (K^*) and of site conditions on the potentially mediating variables. Black arrows indicate significant, dashed arrows marginally significant and faded arrows non-significant relations. Numbers on arrows indicate standardised path coefficients (for unstandardised path coefficients see Table S4) with significance level (.: $p < 0.10$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$), and percentages indicate the variance explained by the model

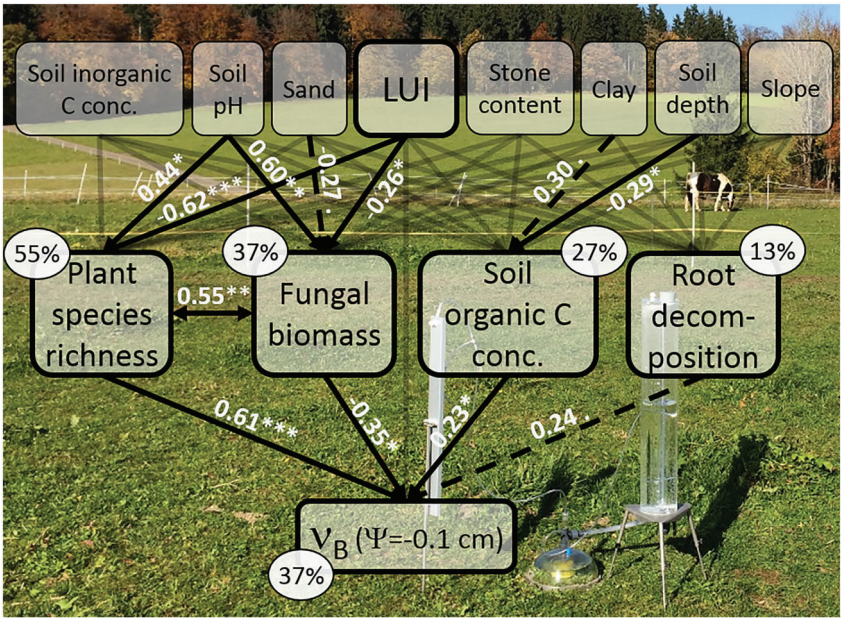

FIGURE 4 Structural equation model (SEM) of the effect of land-use intensity (LUI) via selected variables on infiltration capacity (ν_B) at matrix potential $\Psi = -0.1$ cm and of site conditions on the potentially mediating variables. Black arrows indicate significant, dashed arrows marginally significant, and faded arrows non-significant relations. Numbers on arrows indicate standardised path coefficients (for unstandardised path coefficients see Table S5) with significance level (.: $p < 0.10$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$), and percentages indicate the variance explained by the model

at $\Psi = -0.1$ cm were similar and highly correlated (Table S3) as they differ only by a small change in the matrix potential. Our measurements of ν_B at $\Psi = -0.1$ and -2.0 cm are comparable to the values reported by Fisher et al. (2014, 2015) obtained with the same method on sandy loam to silty clay soils. For K_u at $\Psi = -4.0$ cm and ν_B at $\Psi = -6.0$ cm, only 14 and 15 measurements, respectively, were available because the bubble point of the soil of the other plots was too high to measure infiltration capacity at $\Psi = -6.0$ cm. This low number of samples limits the explanatory power of the statistical analyses. Therefore, we focus on the other matrix potentials in the discussion.

4.1 | Land-use intensity

The negative effects of mowing intensity and fertilising intensity on ν_B, K^*, and K_u (Figure 1 and Table S2) were expected because of the use of heavy machines for fertiliser application and mowing, which lead to soil compaction and a destruction of macropores (Ankeney et al. 1990). However, this explanation was not supported by our results as bulk density did neither significantly correlate with ν_B, K^*, and K_u (Table S2) nor with any of the investigated land-use intensity variables ($p > 0.31$). This indicates that either bulk density is not a good indicator of soil compaction and destruction of macropores or there

must be other processes mediating the effects of mowing intensity and fertilising intensity on ν_B, K^*, and K_u. Grazing intensity significantly increased ν_B at $\Psi = -2.0$ and -4.0 cm and thus counteracted the effects of mowing and fertilising intensity (Table S2). This is contrary to what would be expected from the finding that especially heavy grazing leads to soil compaction through animal treading and thus decreases the infiltration capacity (at saturation) of the soil (Fatichi et al. 2014; Gifford & Hawkins, 1978; Leitinger et al. 2010). While we are aware of one study that reported no effect of grazing (Gifford & Hawkins, 1978), a positive influence of grazing intensity, as at our study sites, has not been reported as far as we know and thus is unexpected. The positive effect of grazing intensity on ν_B at $\Psi = -2.0$ and -4.0 cm might be explained by a positive effect of grazing intensity on soil organic C concentrations and thus increased soil aggregation and decreased bulk density (Fischer et al. 2015; Franzluebbers, 2002). However, soil organic C concentrations were not significantly correlated with ν_B, K^*, and K_u (Table S2) and only for ν_B at $\Psi = -0.1$ cm selected as explanatory variable in combination with other variables in our study (Table 3). Thus, the process behind the positive relationship between grazing intensity and ν_B remains unclear. The negative effect of land-use intensity, measured as LUI, mainly followed the negative effects of its components mowing intensity and fertilising intensity on ν_B, K^*, and K_u (Figure 1 and Table S2). The detected land-use intensity effects on ν_B, K^*, and K_u could originate from confounding influences of site properties that determine land-use intensity. For example, specifically intense land-use measures might have been only applied to sites with less stones, minor slopes, higher soil pH, or specific soil texture. As the mentioned site properties did not correlate with ν_B, K^*, and K_u in our study (Table S2), we can exclude a confounding influence of these properties on the detected land-use intensity effects.

4.2 | Plants and soil animals

We detected a strong positive effect of plant species richness on ν_B, K^*, and K_u (Figure 2a and Tables 3 and S2), which complies with findings for ν_B at $\Psi = 0.0$, -2.0 and -4.0 cm from a plant diversity experiment (Fischer et al. 2015) and findings for $\Psi = 0.0$ cm in a chronosequence of community succession in semiarid grassland (Liu et al. 2019). If plant species richness was not selected as explanatory variable in the linear models, the number of grass species (K_u at $\Psi = -2.0$ and -4.0 cm; Figure 2e) or legume species (ν_B at $\Psi = -4.0$ cm; Figure 2j) was selected (except for ν_B at $\Psi = -6.0$ cm). Fischer et al. (2014) reported that ν_B at $\Psi = 0.0$ and -2.0 cm were lower in the presence of grass and higher in the presence of legume species compared to plots without the respective plant functional group. However, these effects were only significant on some measurement dates (Fischer et al., 2014, 2015). In established grassland systems, like our study plots, specific plant functional groups are rarely completely absent. Thus, other measures than presence/absence of plant functional groups need to be used to investigate plant functional group effects. Such alternative measures can be the numbers of species from a specific plant functional group, which, however, might also differently affect ν_B, K^*, and K_u. Plant species richness, number of grass species, and number of legume species (and also number of herb species, and Shannon index of plants) were strongly correlated with each other and all represent measures of plant diversity that positively correlated with ν_B, K^*, and K_u (Table S2). At the same time, grasses are known for their shallow and dense rooting system and the presence of grasses consistently increased root biomass in a long-term biodiversity experiment (Ravenek et al. 2014). These dense root systems might especially increase the number of finer pores in the topsoil that are active at matrix potentials of -2.0 and -4.0 cm and thus explain the selection of number of grass species as explanatory variable of K_u at $\Psi = -2.0$ and -4.0 cm in our study (Table 3). In a grassland biodiversity experiment and a chronosequence of community succession in semiarid grassland, increasing soil organic C concentrations (and to some extent root biomass) and decreasing bulk density with increasing species richness were identified as the processes behind the positive plant species richness effect on ν_B at $\Psi = 0$ cm (Fischer et al. 2015; Liu et al. 2019). In our study, root variables and/or soil organic C concentrations were also selected as explanatory variables in the linear models for ν_B at $\Psi = -0.1$ and -6.0 cm, K^*, and K_u at $\Psi = -0.1$ cm, albeit in addition to plant species richness and fungal biomass. At the same time, plant species richness did not significantly correlate with root decomposition, fine root biomass, and soil organic C concentrations in our study. According to Solly et al. (2013), plant diversity and root biomass were even negatively related in established grassland systems. This indicates that the process behind the plant species richness effect on the infiltration capacity, detected in the experimental grassland and the chronosequence, was superimposed by other effects (e.g., land-use measures) in the established grassland systems of our study. We assume that the species richness effects in established grassland of the Schwäbische Alb are mediated by root properties (e.g., root-length density) which are difficult to measure, especially on a large number of study sites, and were therefore not available for the 50 study plots.

Fungal biomass did not significantly correlate with ν_B, K^*, and K_u at any matrix potential (Table S2), but was selected as explanatory variable for ν_B at $\Psi = -0.1$ and -2.0 cm, K^*, and K_u at $\Psi = -0.1$ cm (Table 3) in combination with other variables. Barto et al. (2010) reported a positive effect of extraradical hyphal length on soil aggregation on 27 sites across Germany (of which 9 overlapped with our study plots), which could be explained by the release of organic glues from the hyphae. Subsequently, higher fungal biomass might lead to more clogging of pores by organic glues and thus to a reduced infiltration capacity and hydraulic conductivity as indicated by the selected linear models (Table 3).

Soil animals were found to have various effects on ν_B, K^*, and K_u. The Shannon index of Myriapoda was selected as an explanatory variable of K^* and K_u at $\Psi = -0.1$ cm. The positive effect of a diverse Myriapoda community on hydraulic conductivity at or very close to saturation is probably caused by a higher number of macropores for which Myriapoda might serve as an indicator. At $\Psi = -2.0$ and -4.0 cm, the Shannon index of Myriapoda is replaced by the abundance of Pauropoda, a subgroup of the Myriapoda, as explanatory

variable of the hydraulic conductivity (Table 3). Pauropoda are small, cylindric animals with a length of 0.5 to 2 mm. Their size fits to the maximal size of the pores that are potentially active at $\Psi = -2.0$ cm (pores up to an approximate equivalent diameter of 1.5 mm) and -4.0 cm (pores up to an approximate equivalent diameter of 0.75 mm). It is unlikely that Pauropoda create soil pores themselves (Starling, 1944), but their abundance might serve as an indicator of the occurrence of pore sizes equivalent to their body sizes. This might explain the positive effect of Pauropoda on hydraulic conductivity at $\Psi = -2.0$ and -4.0 cm. The absence of an effect of earthworm abundance on ν_B at $\Psi = -0.1$ and -2.0 cm coincides with the findings of Fischer et al. (2014) in fall, which is the same season in which our measurements were performed. In spring, earthworms were reported to increase infiltration capacity at saturation because of their comparatively large casts that serve as macropores and thus increase infiltration capacity (Bardgett, 2005; Fischer et al., 2014, 2015). At $\psi = -2.0$ and -4.0 cm, respectively, we found a negative effect of earthworm abundance on K_u and ν_B, respectively (Figure 2i). As earthworm casts are usually larger than the approximate equivalent diameter of 1.5 mm, which represents the largest active pores at $\psi = -2.0$ cm, and the detected effect of earthworms was negative, the earthworm effect cannot be explained by more (macro-) pores with increasing earthworm abundance. It is known that earthworms contribute to soil aggregation (Blume et al. 2016) and thus might reduce the number of smaller pores that are active at $\psi = -2.0$ cm and -4.0 cm, respectively, and subsequently reduce K_u and ν_B, respectively. Finally, the centipede abundance was selected as explanatory variable of ν_B at $\Psi = -6.0$ cm with a negative effect. Possibly, their faeces lead to clogging of fine pores and thus to a reduction of ν_B at $\Psi = -6.0$ cm.

4.3 | Mediators of detected relationships

In contrast to our hypothesis, the detected effects of land-use intensity on ν_B, K^*, and K_u were not mediated by the physical soil properties total C concentration, bulk density, sand content, stone content, and slope as these properties were neither significantly correlated with ν_B, K^*, and K_u nor selected as explanatory variable in the linear models. Soil organic C concentrations (ν_B at $\Psi = -0.1$ cm), soil inorganic C concentrations (ν_B at $\Psi = -4.0$ cm) and clay content (ν_B at $\Psi = -6.0$ cm) each were selected once as explanatory variable although they did not significantly correlate with ν_B, K^*, and K_u at any matrix potential (Table 3, S2). Soil depth was selected as explanatory variable for and correlated significantly negatively with ν_B at $\Psi = -2.0$ cm. However, LUI did not correlate significantly with soil depth, which might have been the case if soil erosion under high LUI reduced soil depth or if sites with larger soil depth were managed with higher LUI. Therefore, it is implausible that the land-use intensity effect on ν_B is mediated by soil depth.

Our result that soil texture did not affect ν_B, K^*, and K_u (except for ν_B at $\Psi = -6.0$ cm for which clay content was selected in the model selection procedure) is in line with the finding of Fischer et al. (2015). Although soil texture is regarded as a major control of K^* (e.g., in the pedotransfer functions implemented in ROSETTA (Schaap et al. 2001)), this relationship becomes indistinct in the topsoil. The reason for this is that close to the soil surface, the influence of texture on the hydraulic conductivity is superimposed by secondary pores, which can have diverse effects on hydraulic conductivity (Blume et al. 2016). The absence of significant influences or limited impact of soil physical properties on ν_B, K^*, and K_u could be a result of too little variation within the region Schwäbische Alb where all studied soils developed from carbonatic rock under the same climate (see summary statistics of abiotic properties in Table 1).

According to the results of the SEMs, the negative effects of LUI on ν_B at $\Psi = -0.1$ cm and K^* are mainly mediated by plant species richness (Figures 3 and 4). Plant species richness was significantly lower on fertilised than on unfertilised grassland plots of the Schwäbische Alb (Socher et al. 2013), explaining the negative effect of LUI on plant species richness. Fungal biomass is known to decline with increasing land-use intensity in grassland (Bardgett, 2005; Birkhofer et al. 2008), which is reflected in the SEMs (Figures 3 and 4). While the path from fungal biomass to K^* was not significant, the path from fungal biomass to ν_B at $\Psi = -0.1$ cm was significant indicating a negative effect. Thus, the path from LUI to ν_B at $\Psi = -0.1$ cm via fungal biomass represents a positive indirect effect of LUI on ν_B at $\Psi = -0.1$ cm, which counteracts the (stronger) negative effect of LUI via plant species richness. Nitrate concentrations in soil, which are usually higher under high fertilising intensity, were negatively related to the Myriapoda species richness in Central European forest and grassland soils (Birkhofer et al. 2012). Thus, the Shannon index of Myriapoda could have been expected as mediator of the negative land-use intensity effect on K^*, because it serves as an indicator of fertilising intensity. However, the path from LUI to Shannon index of Myriapoda was not significant in the SEM for K^* (Figure 3). The same was true for the soil organic C concentrations in the SEM for ν_B at $\Psi = -0.1$ cm (Figure 4). Root decomposition also did not mediate the effects of LUI on ν_B at $\Psi = -0.1$ cm and K^*, respectively, because the path from LUI to root decomposition was not significant (Figure 4). However, fine root decomposition in grassland was reported to decrease with increasing land-use intensity (in particular N addition) in a study of 150 grassland plots across Central Europe (Solly et al. 2014). A faster root decomposition under lower LUI could lead to more and larger soil pores than in soils with slow root decomposition and thereby increase infiltration capacity and hydraulic conductivity. Together with the result that biotic variables predicted K^* better than it was possible with ROSETTA using soil texture and bulk density (Figure S2), we conclude that plant species richness seems to be a better predictor of K^* than land-use intensity alone or soil physical properties in the established grassland systems of the Schwäbische Alb.

5 | CONCLUSIONS

(1) Supporting our first hypothesis, land-use intensity decreased infiltration capacity and hydraulic conductivity at several matrix

potentials of grassland soils in the Schwäbische Alb. However, this effect was not the strongest detected relationship and could not be attributed to more compacted soil under high land-use intensity.

(2) In line with results of a biodiversity experiment where plant species richness was manipulated, we detected a strong positive effect of plant species richness on infiltration capacity and hydraulic conductivity at several matrix potentials. Furthermore, we showed that the diversity (Shannon index of Myriapoda) and abundance of soil animals (earthworms, Pauropoda) affected infiltration capacity and hydraulic conductivity depending on the species and their properties (e.g., body size) at different matrix potentials. This supported our second hypothesis.

(3) In contrast to our third hypothesis, the effect of land-use intensity was not mediated by physical soil properties, but by biotic variables. Actually, land-use intensity decreased infiltration capacity and hydraulic conductivity mainly via a negative effect on plant species richness on the clay-rich study soils. Moreover, a linear model containing biotic variables allowed for a better prediction of the saturated hydraulic conductivity than the frequently used abiotic ROSETTA model. Further research is necessary to clarify, if these results can be transferred to other regions with, for example, different geological setting and soil properties.

We conclude that land management preserving plant diversity can reduce surface runoff, associated soil erosion, and flooding risks because of the improved infiltration capacity and hydraulic conductivity.

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DATA AVAILABILITY STATEMENT

The infiltration capacity and hydraulic conductivity dataset is published in Leimer & Wilcke (2021). Other data are available on request from the authors and deposited in the online data repository BExIS (http://doi.org/10.17616/R32P9Q), where these will become publicly available after 3 years.

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